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Observations on the Development
of the Trigeminal Nerve
in the Chick

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**OBSERVATIONS ON THE DEVELOPMENT
OF THE TRIGEMINAL NERVE
IN THE CHICK**

BY
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**THESIS FOR
THE DEGREE OF MASTER OF ARTS
IN ZOOLOGY**

**IN THE
GRADUATE SCHOOL
OF THE
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IS APPROVED BY ME AS FULFILLING THIS PART OF THE REQUIREMENTS FOR THE

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I. Introduction.

The development of the trigeminal nerve has never been thoroughly studied and described. Though one of the most constant, this is also one of the most complicated nerves of the head. Professor Minot, in his book on human embryology, says, "No satisfactory observations on the growth of the branches are known to me. The subject would well repay a careful investigation;" and Dr. J. B. Johnston, in his recent work on the nervous system of vertebrates, says that, with the exception of the ciliary ganglion, the development of the sympathetic ganglia connected with the trigemini, has not been directly followed.

The materials used in this study were chick embryos obtained from the incubation of eggs selected without regard to breed, and the heads of adult fowls procured at the poultry house. Examination of transverse and sagittal series proved that the latter were, at all stages of development, the better for showing the trigemini. An attempt was made to select such stages for the drawings and description as would show the consecutive changes that take place and give a connected history of the whole. The stains used were haematoxylin and eosin for larger structures, and, for the finer ones, either iron haematoxylin or vom Rath's fluid.

During the work I have had the supervision and assistance of Dr. F. W. Carpenter, and the use of his collection of chick embryo series.

II. The Adult Trigeminal.

The trigeminal nerve, so named for its three principal branches, is one of the most constant in size and distribution of all the cranial nerves in the vertebrate series. This is because of the permanency of those regions which it supplies. In the fowl it is, after the optic nerve, the largest cranial nerve, and is mixed in nature, having permanently both sensory and motor roots. Its ganglion, the Gasserian, sends out the ophthalmic branch anteriorly to the region of the comb, nasal chamber and beak, the maxillary branch to the upper jaw, and the mandibular branch to the lower jaw (Plate I).

The trigeminal has repeatedly been compared to a spinal nerve it being a natural supposition that Metamerism, so pronounced in the body of the vertebrate, should also exist in the head. In this comparison the two roots of the trigeminal correspond to the dorsal and ventral roots of the spinal nerve, the Gasserian ganglion to the spinal ganglion, and a portion, at least, of the ciliary ganglion, to a typical ganglion of the sympathetic chain.

Opposed to this view may be mentioned Marshall (93), who believes that further investigation will reveal the fact that in the chick, the motor root is not a part of the original nerve but arises independently. McMurrich (1903) has called attention to the double metamerism of the head as a result of which we must account for three sets of nerve roots, two motor roots for the two sets of muscles and one dorsal or sensory root. He therefore believes that little benefit can result from attempts to homologize cranial and spinal nerves.

Again, it has often been said that the trigeminus is homologous with branchial nerves such as supply the gill region of some fishes (Johnston :06) According to this idea the maxillary nerve corresponds to the pretrematic and the mandibular to the posttrematic branches of the branchial nerve, the ophthalmic having no homology in the system. Minot does not share this belief.

The adult condition as revealed by dissection of the fowl's head will now be discussed in some detail, beginning with the origin of the nerve and including branches and ganglia.

The trigeminus is a typical cranial nerve arising from the medulla oblongata by a dorsal and a ventral root. The dorsal root or "portio major" is the larger of the two. It contains the sensory elements and because it extends up into the brain it is often called the ascending root. It originates from ganglion cells in the Gasserian ganglion and enters the brain from the ventral side, where it passes between the dorsal and ventral zones of His, and then, remaining quite near the surface, takes a longitudinal course as a bundle of fibres homologous with the longitudinal bundle formed by the spinal nerves (Minot '92). The root is oval in section, being flattened laterally (His '88). Allis (:01) found that in *Mustelus laevis*, this root is really double, one rootlet having a deeper, more dorsal origin than the other.

The "portio minor" or ventral root is motor in function. The name, descending root, is applied to it to distinguish it from the ascending root, and because its deep origin is posterior to its superficial origin; but in reality it both develops and transmits impulses in a dorsal direction. Its deep origin is the trigeminal motor nucleus in the lateral column of the cervical

spinal cord. Strong ('90) says some of the fibres come from far down the spinal cord in Amphibia. These motor fibres are larger than those found in the ascending sensory root. They pass on the median side of the Gasserian ganglion and, becoming only partly surrounded by this ganglion, they extend directly out into the maxillary and mandibular branches.

The Gasserian ganglion lies on the ventro-lateral surface of the optic lobe (Plate I) in a shallow depression in the bony wall of the cranium. It comprises two embryonic ganglia, a mesocephalic (called ciliary by Minot and others) and a maxillo-mandibular ganglion. From the mesocephalic or anterior portion, the ophthalmic nerve is given off, and the maxillary and mandibular nerves arise independently from the posterior portion. It will be convenient to consider these nerves in reverse order, that is, beginning with the mandibular nerve.

The mandibular nerve is the largest of the three branches of the trigeminus in the chick. It is of mixed nature and so contains elements from both the portio major and portio minor. It comes from the lower and outer part of the ganglion, and even within the connective tissue covering the ganglion, gives off a branch (Plate I?a) to the parotid salivary gland. Just outside the ganglion it gives off another long straight branch (c) to the angle of the mouth. Then the main branch, after supplying the large jaw muscles (o) at the side of the head, passes ventrally and laterally into the canal of the lower jaw, in which it runs forward to the tip, sending out numerous branches, some of which supply the skin of the under surface of the jaw, some the taste buds in the mouth, and some, comparable to the various tooth

nerves, the skin on the edges of the lower jaw (Bronn '91).

The maxillary nerve, the smallest of the three, is also of mixed nature. It has its origin near that of the mandibular nerve, and runs through a bony canal to the orbit, where it extends forward as the infraorbital ramus (d) in the loose connective tissue below the eye-ball. Within the orbit it gives off several branches which supply the conjunctiva, the nictitating membrane, the lower eye-lid, and the skin below the eye, and then bifurcates, sending one branch dorsally within the orbit to communicate with a branch of the ophthalmic nerve. The other branch, continuing forward, leaves the orbit through a canal in the bone, and proceeds ventral to the nasal cavities as the alveolar nerve. It gives off the posterior palatine rami (e), and finally reaches the tip of the beak, where its numerous terminal branches to the palate and the outside surface give it a bush-like appearance.

The ophthalmic nerve is more complicated in distribution than either of the other parts of the trigeminus. It arises directly out of the dorsal lobe of the Gasserian ganglion, and is purely sensory. It reaches the posterior part of the orbit through a bony canal, and passes mediad around the eye-ball on the wall of the orbit. In this transit within the orbit it passes through the base of the external rectus muscle, dorsal to the optic nerve and dorsal rectus muscle, and close along the dorsal edge of the internal rectus muscle. In the anterior median angle of the orbit, lying on the lachrymal gland, it divides into the ethmoid branch and the nasal branch.

The ethmoid nerve leaves the orbit through an orifice in the bone above the lachrymal gland, and passes mediad to the ethmoid

bone, along the dorsal edge of which it proceeds forward for about a centimeter, then turns ventrad, and passing below the nasal passage to the vomer bone, it finally reaches the tip of the beak, which it supplies with numerous twigs. In this position along the ethmoid bone it lies very near the ethmoid nerve from the opposite side, and again near the vomer the two come very near each other and sometimes join (Bronn '91). A branch given off anteriorly near the ethmoid bone, supplies the beak over the nostril.

The nasal branch, or ramus externus of the ophthalmic nerve, divides immediately after its origin, and sends a nerve of considerable size to the skin of the forehead and to the comb. The other part gives off several small nerves to the lachrymal gland and surrounding tissue, and then united within the orbit with the communicating branch of the maxillary nerve already described. It passes in front of the lachrymal bone to the nasal chamber.

In the fowl there are two ganglia in close relation with the ophthalmic nerve. The first or more proximal of these is the ciliary ganglion situated in the orbit near the optic nerve and directly upon the oculomotor nerve. "Two regions are distinguishable in the ganglion, a smaller dorsal region and larger ventral one. The first region presents many sympathetic characters, containing, as it does, small ganglion cells, slightly medullated neuraxons and many pericellular fibrils.----- This communicating ramus from the ophthalmic branch of the trigeminus does not pass directly to the ciliary ganglion, as in the embryo, but to the oculomotor ciliary nerve, with which it connects about one mm. from the distal extremity of the ganglion. Certain of the

neuraxons of the communicating ramus, however, turn centrally and enter the sympathetic region of the ciliary ganglion; the remaining neuraxons accompany those of the oculomotor ciliary nerve to the eyeball."(Carpenter :06).

The other ganglion referred to above is the orbito-nasale ganglion, situated near the ophthalmic nerve just before it divides into the ethmoid nerve and the nasal nerve. It is evidently a sympathetic ganglion, since it consists of a mass of fine fibrils (Plate II, Figure 2) which form the pericellular baskets, and fill the interstices between the cells, obscuring, to some extent, their boundaries and cytoplasm (Plate II, Figure 5). This ganglion lies in the path of the superior ramus of the nervus caroticus cephalicus, a sympathetic nerve coming from the superior cervical ganglion. It communicates with the ophthalmic nerve by a plexus of small nerves (Plate II, Figure 1) in which, as well as in the adjoining part of the ophthalmicus itself, sympathetic ganglion cells are distributed.

Besides this connection with the sympathetic system, the trigeminus communicates more or less regularly, with certain other cranial nerves throughout the vertebrate series. Among these may be mentioned the oculomotor (III), the trochlear or pathetic (IV), the abducent (VI), and the facial (VII) (Hoffmann :02; Coghill :01). Coghill finds that, in Rana, the palatine branch of the facial, or seventh cranial nerve, anastomoses with the maxillary branch of the trigeminus, while in Amblystoma, it is with the ophthalmic branch that this anastomosis takes place, there being no distinct maxillary branch of the trigeminus in Amblystoma.

The preceding description of the trigeminus differs somewhat from that given by Bronn ('91) for Aves in general. Bronn describes a palato-sphenoid ganglion on the maxillary nerve just before it bifurcates, and a consequent connection with the sympathetic system as in mammals. In the specimens of *Gallus domesticus* examined, however, neither this ganglion, nor the communication with the sympathetic system, were found, although microscopic examination was made.

III. Earliest Stages.

The first indication of the trigeminal nerve in the chick is the appearance of the anterior part of the neural ridge at about the twenty-second hour of incubation, or before the neural tube has closed in any part (Marshall '93). In all vertetrate embryos, two ganglia are recognized from the first (Johnston :06). The posterior of these is the Gasserian ganglion or "ganglion maxillo-mandibulare" (Brauer :04), from which develop the sensory portions of the mandibular and maxillary rami. These two rami comprise what is sometimes called the trigeminus proper in contradistinction to the anterior or ophthalmic branch. They receive their motor portions as a direct outgrowth from the neural tube. The anterior ganglion has had a number of names applied to it. Ewart (90) calls it the "ophthalmicus profundus ganglion". It has long been called, in the chick, the ciliary ganglion, and confused with the true ciliary ganglion or the adult which, as Carpenter (:06) points out, is the ganglion connected with the oculomotor nerve. The name "mesocephalic" proposed by Beard ('87), and subsequently employed by Dohrn, Neal, and Carpenter, seems to be the most distinctive and therefore the best name yet applied to this ganglion from which proceeds the first or ophthalmic branch of the trigeminus.

It is generally stated that these ganglia of the trigeminus arise from the most anterior part of the neural crest opposite the anterior vesicle of the hind brain, and later fuse to form the ganglion semilunare (Gasserian) (van Wijhe '82; Beard '87; Marshall '93; Neal '98). According to Johnston (06) these two

ganglia are derived from the neural crest in somites V and VI, and are homologous with dorsal ganglia of spinal nerves. Marshall ('93) points out that the trigeminus of the frog and the chick differs from the dorsal root of a spinal nerve in acquiring a new connection with surface epiblast, and McMurrich (:03) even doubts that any such homology exists. Beard ('85) was the first to observe that the Gasserian ganglion unites with an independently arising knob of ectoderm, from which it receives reinforcement. Brauer (:04) found in *Hypogeophis* that the G. maxillo-mandibulare comes from the dorsal part of the neural ridge, while the G. ophthalmicum develops from only the epidermis, without any contribution from the neural ridge. He says the double origin of such a ganglion in other animals rests perhaps upon deceptive appearances, and thinks that the ophthalmic nerve is more nearly comparable to the olfactory or optic nerve than to the dorsal root of a spinal nerve. According to Giglio-Tos (:02) the final Gasserian ganglion, in man, arises by the union of "3 progangli primitivi neurali, 3 progangli mesocefalici (epibranchiali), e 3 pronervi branchiali."

However the maxillo-mandibulare and the mesocephalic ganglia arise, it is generally agreed that they fuse with each other to form the ganglion semilunare or the Gasserian ganglion of the adult. This has been seen in *Gymnophiona* by Brauer (:04), in guinea-pigs by Chiarugi ('94, '97) and in man by Ewart ('90). In some lower vertebrates they remain separate, as in cyclostomes (Dohrn '88; von Kupffer '95), ganoids (Allis '97), and reptiles (Hoffmann '85).

IV. Seventy-four and one-half Hours' Stage.

Even at this early stage the trigeminal nerve is quite strongly developed (Plate III, Figure 1). It is easily divisible into two principal parts, the ophthalmic and the maxillo-mandibular, each of which has projecting along it for some distance a lobe of the Gasserian ganglion, giving to that ganglion the characteristic angular appearance described by His ('88) for young human embryos.

The Gasserian ganglion is at this time already connected by its centripetal fibres with the brain. This attachment, though probably homologous with the dorsal root of a spinal nerve, is now ventrally situated, a condition characteristic of the nerve-root in the adult. This irregularity is apparently due to the unequal growth of the dorsal and ventral portions of the hind brain, the dorsal part growing so rapidly that the root of attachment becomes shifted farther downward toward the ventral surface of the brain. Marshall ('93), in speaking of the trigeminal nerve of the chick, says the permanent attachment is acquired at the commencement of the third day, and is at the side of the hind brain, becoming subsequently shifted ventrally.

At 74 1/2 hours' incubation, the maxillo-mandibular nerve comes off from its portion of the Gasserian ganglion as a very thick fibrous stem devoid of ganglion cells. It reaches far out in the mandibular arch toward the median line of the animal, and ends abruptly without branches. There is as yet no indication of the separation of this stalk into a maxillary and a mandibular nerve, which division takes place somewhat later as we shall presently see.

The ophthalmic nerve extends dorsal to the optic stalk toward the fore-brain, and is quite complicated. It has several branches which anastomose with each other, and which contain among their fibres ganglion cells resembling those seen in the Gasserian ganglion itself. These ganglion cells along the nerve are grouped into four loosely defined clumps or ganglia (Plate III, Figure 1, 1,2,3,4), from which terminal branches are given off. The first of these ganglia is located in a position later occupied by the ciliary ganglion, to which it may very likely contribute cells, but there is as yet no connection between this ganglion and the oculomotor nerve. This embryonic ganglion is connected with the ophthalmic portion of the Gasserian ganglion by two communicating rami, the one median to the other, and both containing ganglion cells among their fibres. An oblique section through the dorsal portion of this ganglion is shown with higher magnification in Plate II, Figure 3. The contained ganglion cells are somewhat larger than those seen in other parts of the nerve, and are quite easily distinguishable, with the vom Rath stain, from the accompanying cells with which the nerve is crowded.

Just as the ophthalmic nerve crosses the optic stalk it divides into two principal branches on the dorsal of which are located the second and third ganglia. Ganglion number three is large and conspicuous, being about half the size of the mesocephalic. It is situated close up under the fore brain. Here again the size of the contained ganglion cells attracts the attention, but this time they are smaller than the cells in the distal part, at least, of the mesocephalic ganglion. From this ganglion a stem runs across and meets the ventral of the principal branches

mentioned above and at this junction the fourth of the embryonic ganglia is situated.

The terminal rami given off are, two (a & b) from ganglion number three, one running backwards and the other forwards close to the fore brain, one (c) from ganglion number four, which extends dorsal or anterior to the eye-stalk into the frontal region, and two (d & e) from ganglion number one, which turn up toward the eye-stalk from the ventral or posterior side. One of these last (d) is so distinct under oil immersion lens, that I have made a camera lucida projection of it (Plate III, Figure 2), thinking that it might in a way reply to the challenge made by Cameron (:06) to describe the growing end of a nerve fibre.

The series was stained after the vom Rath method, and this drawing is reconstructed from two adjacent sections. In one of them, the heavier part of the nerve was traced past the blood vessel to region opposite "x", where all but one of the fibres of the tangled mass had disappeared. Although this fibre followed a very tortuous course it could very easily be traced out beyond all the other fibres, where it lay between two rows of cells and disappeared abruptly at "x". In the next section a single wavy fibre appeared at about the region "x", and could be traced farther into the mesenchyme, where it seemed to grow somewhat smaller and stop again rather abruptly. Succeeding and preceding sections showed no further trace of this fibre. While one cannot say positively that this is the end of the growing nerve fibre, yet it appears to be, since, although the single fibre was traced easily in two successive sections, it does not appear at all in the next following section.

An interesting thing to notice about this growing nerve end is the arrangement of cells along the nerve. From a thick region in which ganglion cells and other cells are mingled among numerous fibres we pass to a region in which the single remaining fibre lies between cells lined up on either side, thus producing an accumulation of material which one can trace under low power; thence to the extreme end of the fibre, which lies free in the mesenchyme without any condensation of mesenchymatous material about it. Each fibre appears to be made up of fibrillae. Ganglion cells usually have their nuclei eccentrically placed, and when their cytoplasm is drawn out into a point, this point may project either back toward the brain or toward the distal extremity of the nerve. The striated appearance characteristic of the embryonic nerve under medium high power, is produced by the mass of more or less tangled fibres.

V. One hundred one Hours' Stage.

In sections of the trigeminus made at the one hundred and first hour of incubation (Plate IV), the Gasserian ganglion and maxillo-mandibular branch appear about the same as at seventy four and one-half hours, except that the latter is even more massive than before. It is still without ganglia or ganglion cells, and is much longer than appears in the drawing, because it bends to follow the arch in a manner which cannot be shown in sections made in sagittal planes. In the ophthalmic nerve, however, we find that quite a change in appearance has taken place. Its division into two principal branches above the eye-stalk remains the same, but its ganglia and terminal rami have undergone modification. Ganglion number one of the seventy-four and one-half hours' stage has been greatly reduced. The distal end of the developing oculomotor nerve is now in the immediate vicinity of this ganglion. Ganglia two, three, and four, of the seventy-four and one-half hours' stage, which were from the first only partially differentiated from each other, seem to have coalesced into one large ganglion which lies antero-dorso-median to the optic cup and quite near it. There is also now a new ganglion situated on that terminal ramus (b) of the previous stage, which runs forward below the fore-brain. From this ganglion the branch continues dorsally for a short distance in front of the fore-brain. Terminal branch "a" of the earlier stage is much reduced, and "d" and "e" are lost. Rami "b" and "c" now lie very close together, the latter being the more median in position, and extending out over the optic cup almost to the ectoderm.

VI. One Hundred Eighteen Hours' Stage.

This stage shows changes in every part of the trigeminus. The massive Gasserian ganglion with its two prongs, the mesocephalic and maxillo-mandibular ganglia, has a very noticeable horseshoe shape, and it is this appearance which gives it the name ganglion semilunare (Plate V). The ganglion cells in that portion of the ganglion nearest the brain are smaller than those farther out in the prongs.

There are now distinct maxillary and mandibular nerves. The maxillary arises as a branch of the mandibular at a point near the outer extremity of the Gasserian ganglion, and then splits centrally into the ganglion, so that it finally appears to arise as a separate nerve. This was observed for vertebrates generally by Kupffer ('91). In the series examined, this maxillary branch first appeared on the fifth day, although Marshall ('93) says, in speaking of the trigeminus of the chick, "by the end of the third day or early on the fourth day, its main branches of distribution become definitely established. From the mandibular nerve, the maxillary nerve arises as a branch which runs forwards in the maxillary arch or upper jaw."

These two rami may be compared to the pretrematic and post-trematic rami of the typical branchial nerve of lower vertebrates, the mouth taking the place of a branchial cleft (Johnston :06). Minot ('92) thinks that if the mouth in the human embryo be interpreted as representing a pair of gill clefts, then the trigeminus may be interpreted as the nerve of that cleft, and its two branches, one in front of, the other behind the mouth, may be compared with the branches of the branchial nerves, but he suggests the probab-

ity that they are distinct nerves and their union secondary, and that these theoretical considerations have had undue influence in forming the view usually favored, that they are primitive branches.

The maxillary nerve at this stage is quite slender as compared with the mandibular from which it grows. It passes near the lower border of the optic cup, which is now very large, and extends far out into the maxillary process. It contains no ganglion cells.

The mandibular nerve, a thick bundle of fibres, ends very abruptly except for a few small branches (Plate V, x,y,z) toward the angle formed by the mandibular arch and the maxillary process. One of these small branches arises near the maxillary nerve and extends somewhat parallel to that nerve, but is much more externally situated (x).

The ophthalmic nerve has at this one hundred eighteenth hour, no ganglia whatever along its main stem. The ciliary ganglion is now quite well developed. Many of its ganglion cells are much smaller than those along the ophthalmic nerve or in the Gasserian ganglion. It lies directly on the oculomotor nerve with a communicating branch, the ramus nasociliaris of the adult, connecting it with the ophthalmic nerve near the mesocephalic ganglion. This ramus nasociliaris consists of fibres rich in large oval ganglion cells which appear to be migrating from the Gasserian ganglion. It connects with the ciliary ganglion directly instead of indirectly as in the adult.

From here the ophthalmic nerve turns mediad to avoid the large optic cup, on the wall of which it runs forward, dorsal to the optic stalk, around to the frontal region, where it breaks up,

at a point opposite the outer border of the cup, into a number of small branches (Plate V, a,b,c), the longest one of which turns ventrad and extends down in front of the optic cup, where it comes almost into contact with the nasal pit.

Lying in the mesenchyme near the ophthalmicus at the place where it breaks up into the branches just mentioned, may be seen a small isolated patch of nerve tissue with two or three well defined ganglion cells (Plate V, 1,2,3).

As the main branch passes by the optic stalk, it gives off two branches of considerable size, a ventral one (d) without ganglion cells, which runs around the stalk to the front, and a dorsal one (e), rich in ganglion cells, especially at its distal extremity, where they are collected into a minute compact ganglion (4), from which radiate short bits of nerve fibres.

There are a few other ganglion cells scattered along the main stem from the mesocephalic ganglion, but they extend only as far as "5". At no place is the number of these at all comparable to the number seen along the ophthalmic nerve at earlier stages.

VII. One Hundred Forty-three and one-half Hours' Stage

The distinguishing feature about this stage in the development of the trigeminal nerve is that its motor root, or protio minor, now becomes easily recognizable. It is developed as a bundle of nerve fibres from neuroblasts of the ventral zone of His in the hind brain, and makes its exit near the dorso-lateral edge of this zone. This group of neuroblasts or trigeminal nucleus, as it is called, lies near the junction of the dorsal and ventral columns and, therefore, close to the ascending sensory root of the trigeminus (His '88). This motor path, in the series examined, could be traced through the Gasserian ganglion near its median side, where the fibres did not mingle with the ganglion cells, out into the maxillary and mandibular branches.

The Gasserian ganglion and the three principal branches given off from it, are now somewhat similar to those found in the adult (Plate VI). The ganglion has a short but distinct stem of fibres by which it is attached to the brain. It is distinctly bi-lobed, sending off the ophthalmic branch from the anterior, and the maxillary and mandibular branches from the posterior lobe.

All three branches arise directly from the ganglion, the mandibular coming off lateral and somewhat posterior to the origin of the maxillary. Both these last named branches are without ganglion cells beyond the Gasserian ganglion. The mandibular branch is much reduced in width from its former condition. It follows the mandibular arch and sends a branch toward the angle of that arch and the maxillary process. The maxillary lies close under

the eye, and divides into two branches, one of which runs a short distance dorsally in front of the optic cup.

The ophthalmic branch is more simple in its make-up than it was in previous stages. It extends as a slender, compact nerve out toward the optic cup, near which it gives off its communicating ramus to the ciliary ganglion. It then turns more dorsad and mediad, around the cup, until it comes quite near to its fellow from the other side in the median plane of the body directly between the optic cups. Still keeping near the cup it runs laterad to the frontal region, where it breaks into two branches, one of which (Plate VI, f) runs medio-dorsally for a short distance, and the other (e) latero-ventrally in front of the eye, where it ends blindly, lateral to the olfactory invagination.

There are a few embryonic ganglion cells scattered along the nerve at its proximal end, but none at the point of attachment of the branch which communicates with the ciliary ganglion. All transitory ganglia and scattered cells distal to this point have disappeared except two small groups (1 & 2) above the eye, which are not large enough to cause any distention of the nerve. The distal of these two groups is located near the point where the future attachment of the sympathetic nerve will take place, just before the nerve divides into its two principal branches.

An oblique section through the first or proximal of these two groups is drawn from greater magnification to show the characteristic appearance of an embryonic nerve with ganglion cells lying among its fibres (Plate II, Figure 4). This magnification was obtained with a Bausch and Lomb one-fourth objective, and is sufficient to show that the fibres are roughly arranged in bundles

which seem to anastomose with each other, forming meshes in which the ganglion cells and numerous other cells lie. The series was stained with iron haematoxylin. This gave a deep blue color to the cytoplasm of these embryonic ganglion cells and to the chromatin matter contained in their nuclei. The cytoplasm is usually collected on one side of the round or oval nucleus. Plate II, Figure 5, shows one of these embryonic cells (a) in comparison with an adult ganglion cell (b) from the orbito-nasale ganglion as it appears in section in Figure 2. Regarding the origin or the fate of the embryonic cells we have no absolutely certain knowledge. The adult cell we believe to be a multipolar sympathetic ganglion cell as has already been stated (Page 8). The two are drawn to the same scale to show the great difference in size. While the embryonic cell has a definite wall the adult cell has not, due perhaps, as has been said before, to its multipolarity, or to the pericellular, intra-capsular basket. The nuclei of the two cells are very similar in size, in nuclear wall, and in chromatin content.

VIII. Discussion.

The history of the development of the trigeminal nerve in the chick may be briefly summed up as follows:- At the end of the first day of incubation the neural ridge appears, from which the Gasserian ganglion develops in two parts, the anterior or mesocephalic ganglion, from which the ophthalmic branch extends, and the posterior or maxillo-mandibular ganglion, from which grows out the maxillo-mandibular nerve. The motor root arising near the sensory one becomes strongly developed by the sixth day, and sends fibres along the inner side of the Gasserian ganglion into the maxillary and mandibular nerves, but not into the ophthalmic nerve. The maxillary becomes separated off from the mandibular on the fifth day (Kupffer '91), the former developing along the maxillary process and the latter along the mandibular arch. Both are devoid of ganglion cells.

The ophthalmic nerve is, from the first, more changeable in its development than the other two branches. It crosses dorsal to the optic stalk and, by the end of the fifth day, has almost reached the olfactory invagination. It produces many vigorous branches and ganglia which are afterwards entirely lost.

The ramus communicating with the ciliary ganglion first arises quite near the Gasserian ganglion and extends directly into the embryonic ciliary ganglion. Later its relation to these changes so that, either by a shifting of attachment or a receding of the Gasserian ganglion, it comes to arise from the ophthalmic nerve at some considerable distance from the Gasserian ganglion, and instead of passing directly to the ciliary ganglion, it connects

with the oculomotor ciliary nerve about one mm. (Carpenter :06) from the distal extremity of the ganglion. From this point of attachment, according to Carpenter, it sends neuraxons both toward the eyeball and back toward the ciliary ganglion.

Regarding the history of the ganglion cells and the indifferent cells which we have seen scattered along the ophthalmic nerve all through its earlier development, there is much speculation. They appear to come from the Gasserian ganglion. There is evidence that some of the indifferent cells become Schwann's-sheath cells of the adult nerve, but the fate of all of them is not so easily explained. Certainly many of them must degenerate. The few scattered ganglion cells near the place where the ophthalmic nerve breaks up in the one hundred eighteen hours' stage (Plate V, 1,2,3) seems to indicate the breaking down of some past aggregation of such cells. From its position, this aggregation may correspond to a certain transitory ganglion described by Rubaschkin (:03). This investigator found, in nine day old embryos of Gallus, a connection between the ophthalmic nerve and an olfactory ganglion situated under the back part of the membrana olfactoria.

It is believed by some that at least part of the ciliary ganglion is made up of cells which have migrated from the Gasserian ganglion (Marshall '93; Carpenter :06). Their distribution as we saw it in Plates III, IV, & V, would seem to substantiate this belief. In this connection, van Wijhe ('82) thinks that, in the separation of the ciliary ganglion from the Gasserian in Selachians, a considerable middle portion of the originally continuous ganglionic mass disappears. His ('88) tells us that in the human embryo at one month the ciliary ganglion is connected with the

trigeminal by a bundle of fibres without cells.

Some derive still other peripheral ganglia from this source. Minot ('92) writes of the Gasserian ganglion in man as follows;- "The peripheral nerves it gives off are accompanied by some of the ganglion cells, which are thought by His to be destined to form the anlagen of the ganglion rhinicum and ganglion oticum", and Marshall ('93) says, on the same subject, "As the ophthalmic, maxillary and mandibular nerves lengthen, the originally single ganglion gradually breaks up, small portions becoming detached, and moving out along the growing nerve stems. In this way, early in the fifth week, the ciliary, spheno-palatine, and otic ganglia are established; the submaxillary ganglion is not separated until a rather later stage."

In the chick, however, it will be remembered that no ganglion cells appear along either the maxillary or mandibular nerves in early embryonic stages. This becomes significant when we consider that there are no ganglia in the adult along these nerves, and gives additional proof that nerve cells, when they do migrate peripherally along nerves, may take part in the formation of peripheral ganglia.

In this connection, attention was called to the fact that in the one hundred forty-three and one-half hours' stage (Plate VI), a group of embryonic ganglion cells (2) has a position which will be occupied by the future orbito-nasale ganglion. This fact, together with the resemblance of the nuclei of the adult ganglion cells of this ganglion to the nuclei of embryonic ganglion cells of late stages (Plate II, Figure 5, a,b), suggests the possibility that the one may develop into the other. Additional evidence is

obtained by noting the distribution, in the adult, of some of the ganglion cells within the ophthalmic nerve itself Plate II, Figure 1). However, the origin of the cells in the adult ganglion we must still leave in doubt. It does not necessarily follow that because there is a clump of ganglion cells along the embryonic ophthalmic nerve, in the approximate position of the adult ganglion, these cells become the ganglion cells of the adult ganglion.

This transitional or temporary nature of so many nerve structures suggests an explanation for another long debated question. The question has been asked over and over again, especially by those who advocate the cell chain theory of nerve origin, as opposed to the cell process theory, how it is possible for a nerve, growing centrifugally, to find its correct termination, or what mysterious chemical, physical, or vital power it is which directs the growth of a neuraxon from a cell in or near the spinal cord or brain, through the heterogeneous mass of tissue to a particular muscle or sense area, perhaps several feet away. Now when this question is asked the assumption is made that the young nerve does grow, without much waste of energy or material, by a more or less direct course, from its source to its termination. On the other hand, as we have seen in the case of the trigeminal nerve, there may be much transitory nervous tissue produced, both cells and fibres; and strong branches and ganglia disappear without leaving a trace behind? Whatever the source of the ganglion cells, it is certainly a very prolific one, and it is possible that the development of the nerve is, to some extent, haphazard, only those parts being retained in the adult which happen to form the structure suitable for a particular function. Accordingly, we may imagine

that many of the nerve cells are lost merely by chance, and that, somehow, functionality is an important factor in determining which shall disappear and which shall persist/ This seeming waste of material and energy is analogous to the great over-production of pollen grains in plants or spermatozoa in animals, each one apparently as good as every other, but few reaching the end for which they were designed.

IX. Summary.

1. The Gasserian ganglion is bi-lobed throughout its development. It consists of an anterior, mesocephalic portion, and a posterior, maxillo-mandibular portion. These develop separately from persisting portions of the neural crest and, shifting ventrally, they fuse and become attached to the ventral side of the hind brain. From the mesocephalic part grows out the ophthalmic nerve, and from the maxillo-mandibular part, the sensory portions of the maxillary and mandibular nerves.

2. The maxillary nerve does not develop directly out of the Gasserian ganglion, but arises as a branch of the mandibular nerve and subsequently shifts its attachment to the ganglion.

3. The motor root of the trigeminus appears on the sixth day of incubation. Its fibres pass on the median side of the Gasserian ganglion without mingling with the cells of that ganglion, and enter the maxillary and mandibular branches.

4. The maxillary and mandibular nerves do not contain, during their development, embryonic ganglion cells peripherally distributed.

5. There are many nerve branches and groups of ganglion cells along the embryonic ophthalmic nerve which are transitional, disappearing before the adult condition is reached.

6. There is evidence that these cells contribute to the formation of the ciliary and orbito-nasale ganglia of the adult, for not only do they accumulate at the places later occupied by the adult ganglia, but their nuclei are very similar to the nuclei of

the ganglion cells in the adult orbito-nasale ganglion and in the sympathetic portion of the ciliary ganglion.

7. The ophthalmic nerve in the adult, passes mediad of the eye-ball, through the orbit, where it communicates with the oculomotor ciliary nerve and with the orbito-nasale ganglion. It divides near the lachrymal gland into an ethmoid nerve, which supplies the upper and distal part of the beak, and a nasal nerve, which sends branches to the forehead, the comb, the lachrymal gland, the nasal chambers and the tip of the beak.

The maxillary nerve also passes through the orbit, lying ventral to the eye-ball, and being distributed to the conjunctiva, the nictitating membrane, the lower eyelid, the skin below the eye, and the upper jaw.

The mandibular nerve sends branches to the parotid salivary gland, the angle of the mouth, and the large jaw muscles, and then passes through a canal in the bone of the lower jaw to its tip, giving off nerves to the inside and outside surfaces of the jaw.

8. In the adult, the maxillary nerve does not communicate with the sympathetic system through a palato-sphenoid ganglion, but the ophthalmic nerve does communicate through the orbito-nasale ganglion with the sympathetic nervous system.

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Plate I. Head of adult Gallus domesticus dissected to show distribution of trigeminal nerve,

a,b,c - branches of mandibular nerve.

d,- infraorbital nerve.

e, - posterior palatine rami.

ex.nar. - external nares.

gn.Gas. - Gasserian ganglion.

gn.orb-nas. - ganglion orbito-nasale.

lach.gl. - lachrymal gland.

mu.ob.d. - dorsal oblique muscle.

mu.ob.v. - ventral oblique muscle.

mu. rt.a. - anterior rectus muscle.

mu.rt.d. - dorsal rectus muscle.

mu.rt.p. - posterior rectus muscle.

mu.rt.v. - ventral rectus muscle.

n.alv. - alveolar nerve.

n.eth. - ethmoid nerve.

n.mand. - mandibular nerve.

n.max. - maxillary nerve.

n.nas. - nasal nerve.

n.opth. - ophthalmic nerve.

n.opt. - optic nerve

n. sympath. - sympathetic nerve.

par.gland - parotid salivary gland.

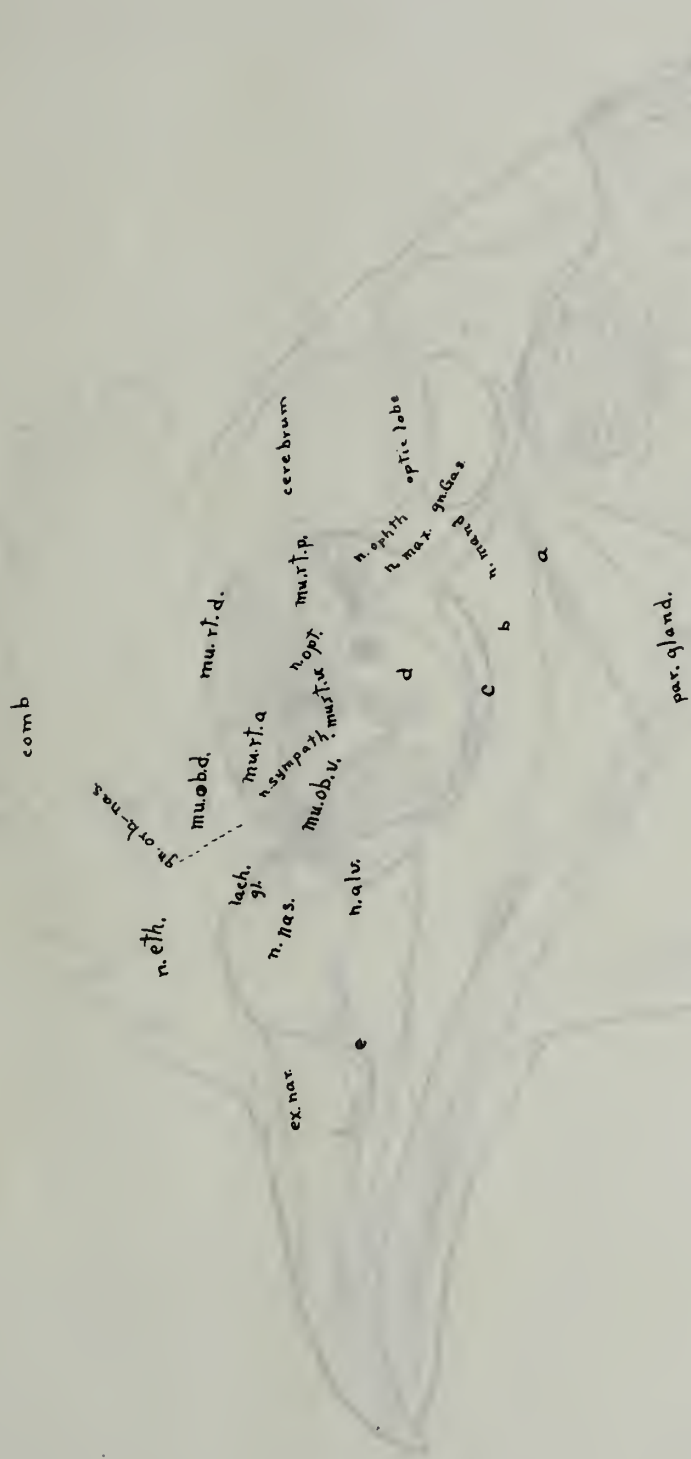


Table 1. Data on 1992-1993 breeding season of the
 American alligator.

1992 - 1993 breeding season

1. 1992-1993 season

2. 1992-1993 season

3. 1992-1993 season

4. 1992-1993 season

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6. 1992-1993 season

7. 1992-1993 season

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13. 1992-1993 season

14. 1992-1993 season

15. 1992-1993 season

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21. 1992-1993 season

22. 1992-1993 season

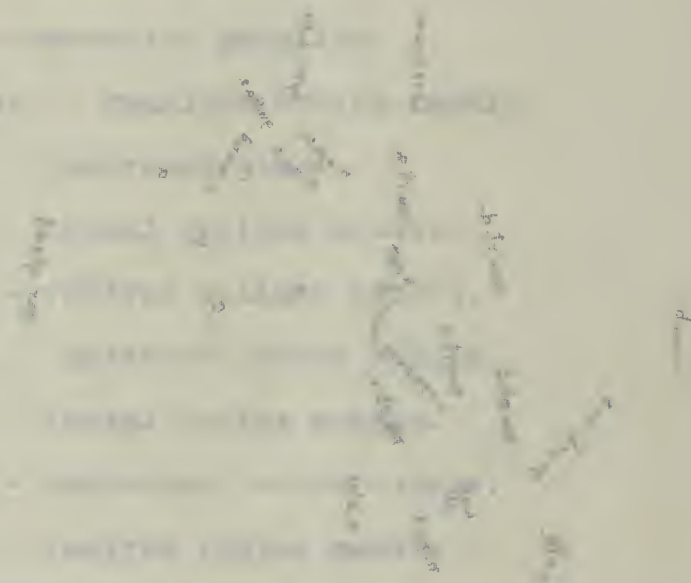


Plate I.



Plate II, Figure 1,- Reconstruction of the orbito-nasale ganglion and its communication with the ophthalmic branch of the trigeminus in adult Gallus domesticus.

xy, - plane of section shown in Figure 2.

gn.orbito-nas. - orbito-nasale ganglion.

n.opth. - ophthalmic nerve.

rm.comn. - communicating ramus.

Figure 2, - Section through the orbito-nasale ganglion and the ophthalmic nerve of the adult, in the plane xy of Figure 1. haematoxylin and eosin. Low power.

cl.gn. - embryonic ganglion cell.

gn.orb-nas. - orbito-nasale ganglion.

n.opth. - ophthalmic nerve.

rm.comn. - communicating ramus.

Figure 3, - Oblique section (49-1-3-5) through the ophthalmic nerve of 74 1/2 hrs. at the point "1" of Plate III, Figure 1. B.&L. 1/4 obj. vom Rath.

cl.comit. - accompanying cells.

cl.gn. - embryonic ganglion cells.

Figure 4, - Oblique section (10-12) through the ophthalmic nerve of 143 1/2 hrs. at the point "1" of Plate VI. Fe-haem.

cl.comit. - accompanying cells.

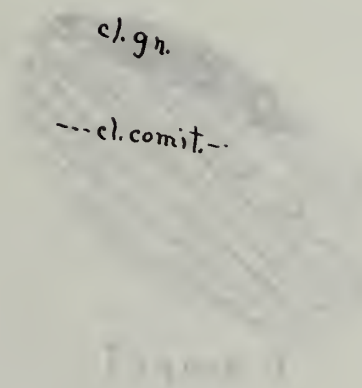
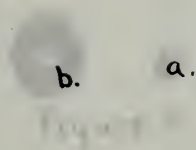
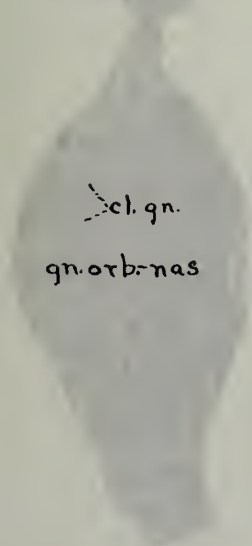
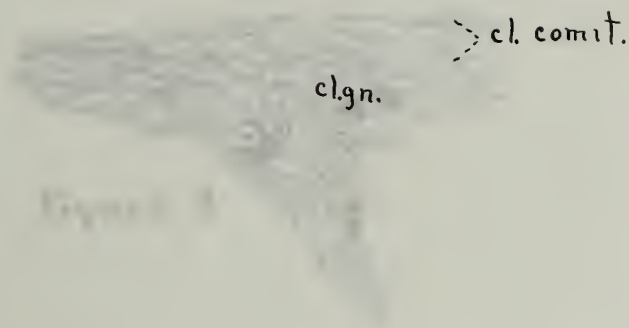
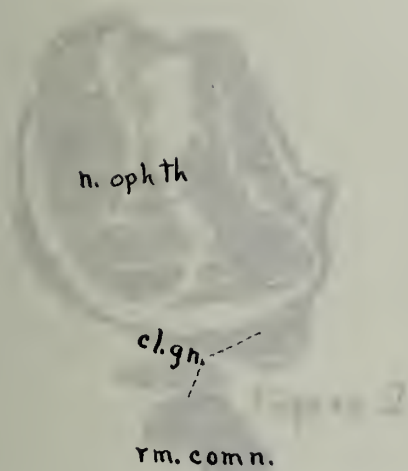
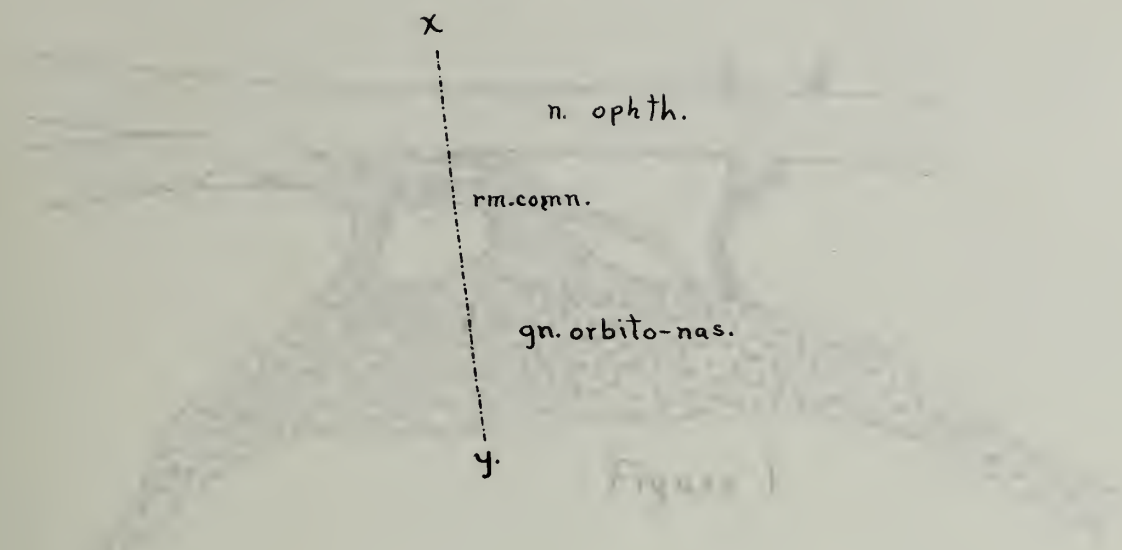
cl.gn. - embryonic ganglion cells.

Figure 5, - Embryonic ganglion cell (a) and adult sympathetic ganglion cell (b) drawn to scale. B & L 1/4 obj.

a. - from the ophthalmic nerve at 143 1/2 hrs. Fe. haem.

b. - from orbito-nasale ganglion shown in Figure 2. H+E.

Plate II



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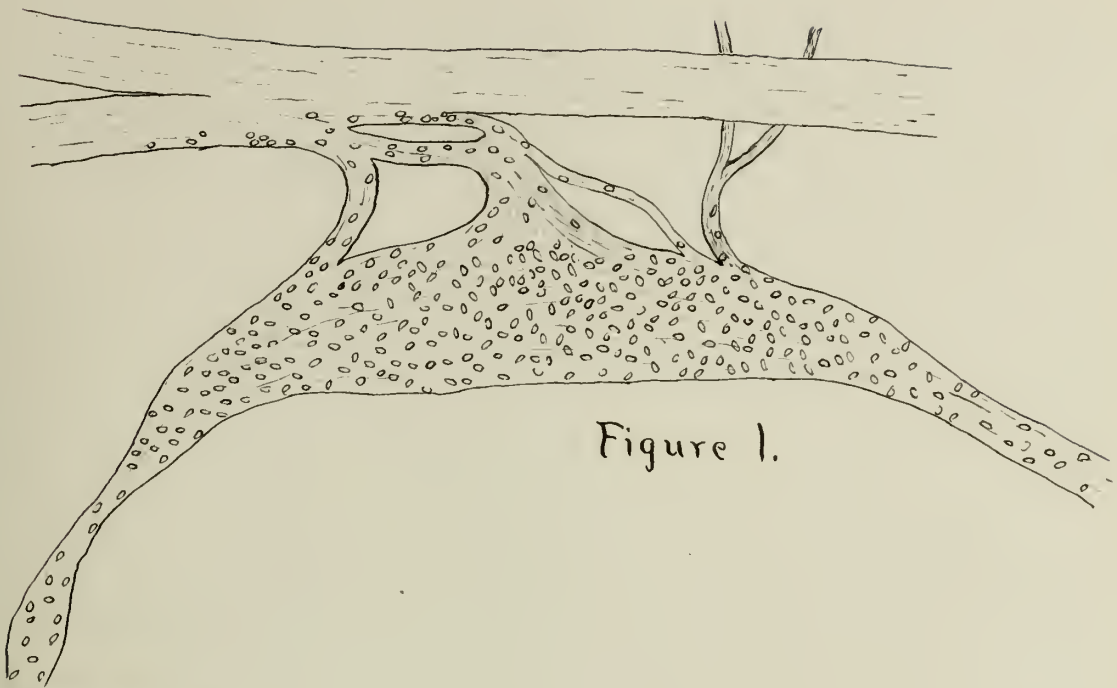


Figure 1.



Figure 2.

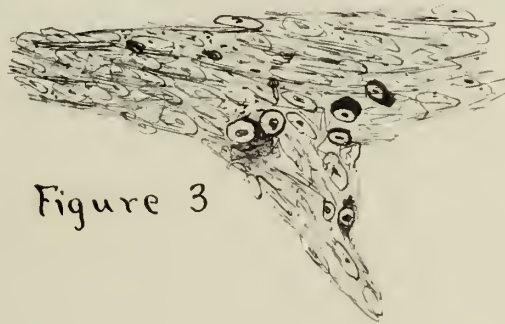
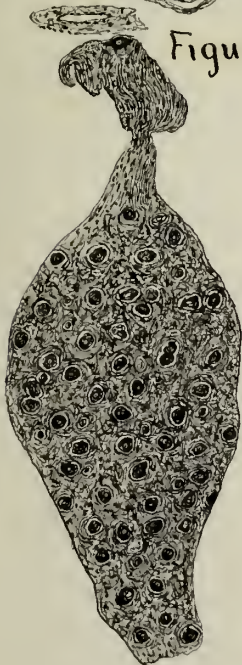


Figure 3



Figure 5'



Figure 4

Plate III. Figure 1, - Diagrammatic representation of the trigeminus at 74 1/2 hours' incubation, stained with vom Rath.

a,b,c,d,e, - terminal rami.

1,2,3,4, - transitional embryonic ganglia.

bl.ves. - blood vessel.

gn.Gasserian - Gasserian ganglion.

gn. mx-md. Gas. - maxillo-mandibular portion of the Gasserian.

gn.opth.Gas. - ophthalmic portion of the Gasserian.

hyoid arch.

mand.arch. - mandibular arch.

max.arch - maxillary arch.

n.max-mand. - maxillo-mandibular nerve.

n.opth. - ophthalmic nerve

Figure 2, Terminal ramus "d" of Figure 1.

Magnification 900 diameters.

bl.ves. - blood vessel, (same one as in Figure 1).

cl.gn. - embryonic ganglion cell.

corp. - corpuscle.

ms'ench. - mesenchyme.

n'ax. - neuraxon.

mid brain

hind
brain

n. ophth.

a.

3.

2.

1.

4.

gn. Gasserian
gn. ophth. Gas.

b1. ves.

gn. mx-md. Gas.

d

e.

optic cup

b.

c.

n. max-mand.

max. proc.

mand. arch

hyoid arch

fore
brain

corp.

b1. ves.

cl. gn.

cl. gn.

ms'ench.

X

nax

mid brain

hind brain

mid brain

an. oblique

max. arch

max. arch

max. arch

max. arch

max. arch

max. arch

max. arch

max. arch

Plate III.

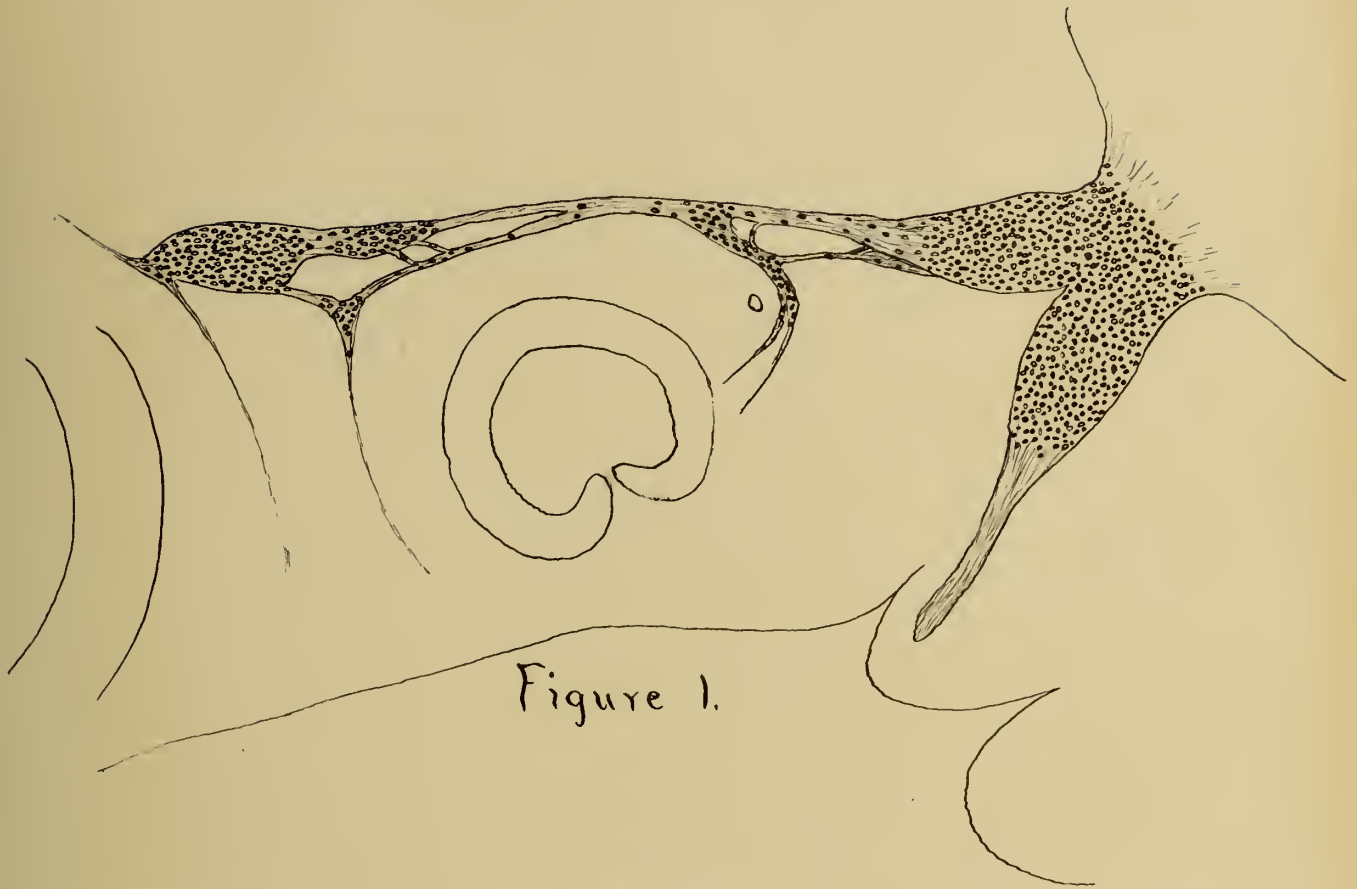


Figure 1.

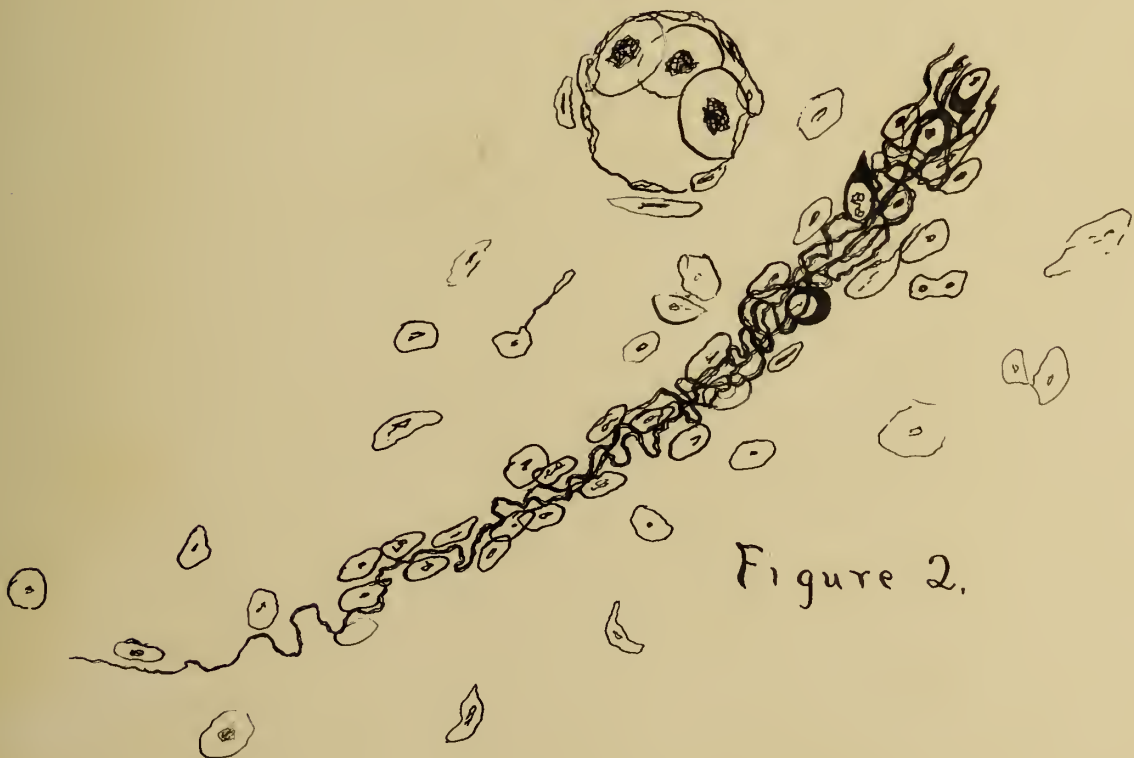


Figure 2.

Plate IV. - The trigeminal nerve at 101 hours' incubation.
Stained with vom Rath.

a,b,c, - terminal rami (same as in Plate III).

1,2, - transitional embryonic ganglia.

gn.cil. - ciliary ganglion.

gn.Gas. - Gasserian ganglion.

gn.mx-md. Gas. - maxillo-mandibular portion of the Gasserian.

gn.opth. - ophthalmic portion of the Gasserian ganglion.

mand.arch - mandibular arch.

max.proc. - maxillary process.

n.mx-md. - maxillo-mandibular nerve.

n.oc'mot. - oculomotor nerve.

n.opth. - ophthalmic nerve.

Plate IV.

mid brain

n. oc'mot.
t.

hind brain

gn. Gas.

gn. ophth.

n. ophth

gn cil.

gn. mx-md. Gas.

n. mx-md.

optic cup

a

1.

b

c

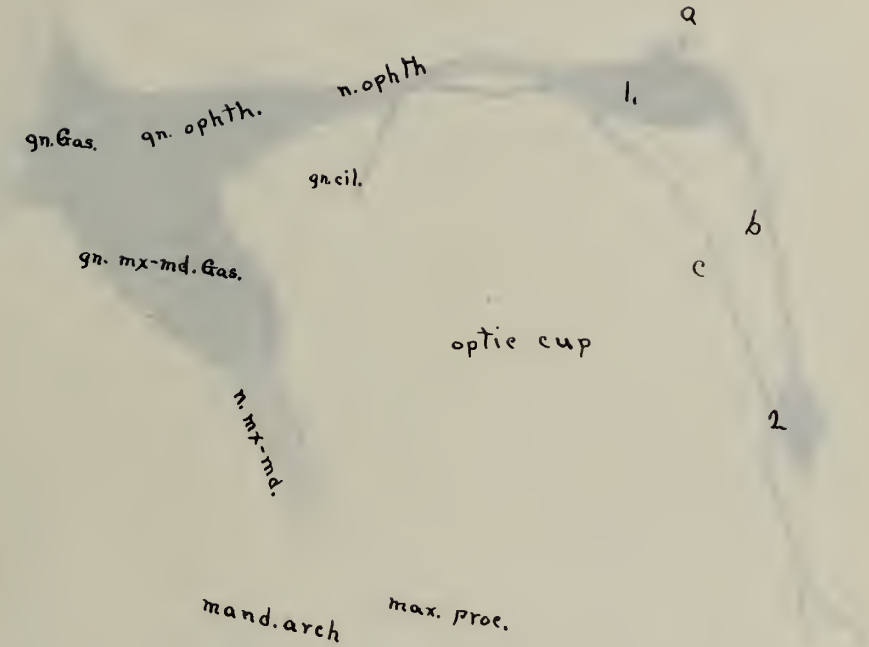
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otocyst

mand. arch

max. proc.

hyoid arch



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1
2
3
4
5

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Plate IV.



Plate V, - The trigeminal nerve at 118 hours' incubation.
Stained with vom Rath. (The section through the large optic
cup lies lateral to the remainder of the structures shown).

a,b,c,d,e, - terminal branches of the ophthalmic nerve.

x,y,z, - terminal branches of the mandibular nerve.

1,2,3,5, - embryonic ganglion cells.

4, - transitional ganglion.

gn.cil. - ciliary ganglion.

gn.Gas. - Gasserian ganglion.

gn.mx-md.Gas. - maxillo-mandibular portion of the Gasserian
ganglion.

gn.opth.Gas. - ophthalmic portion of the Gasserian ganglion.

n.mand. - mandibular nerve.

max.n. - maxillary nerve.

n.oc'mot. - oculomotor nerve.

n.opth. - ophthalmic nerve.

olf.inv. - olfactory invagination.

rm.comn. - communicating ramus.

Plate 2



mixed bird

1000 ft
1000 ft
1000 ft

1000 ft

1000 ft

1000 ft

1000 ft

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1000 ft

Plate V.

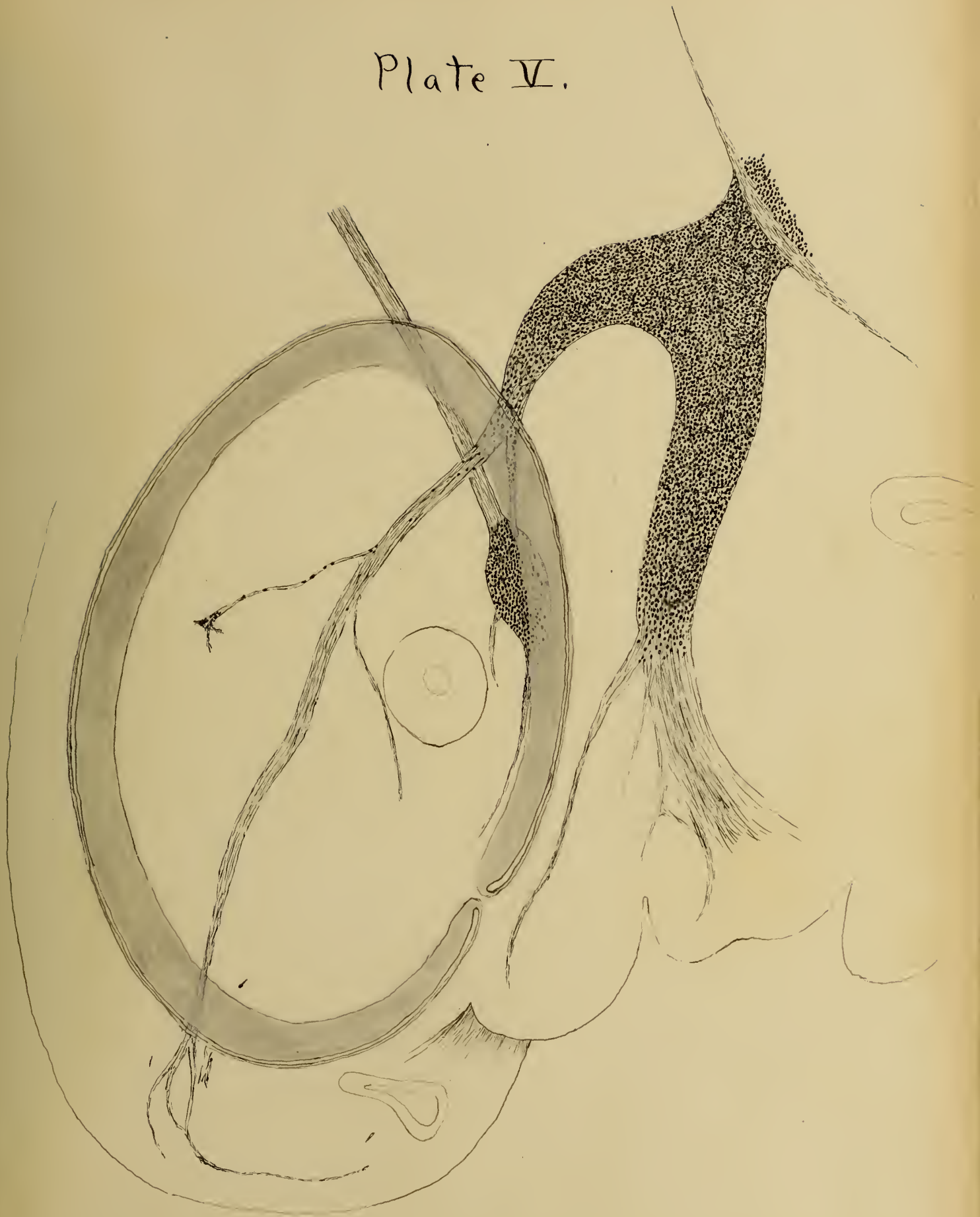


Plate VI, - The trigeminal nerve at 143 1/2 hours' incubation.
Stained with iron haematoxylin.

a,b,c,d,e,f, - terminal branches.

1,2, - groups of ganglion cells.

bl.ves. - blood vessel (median to nerve).

gn.cil. - ciliary ganglion.

gn.Gas. - Gasserian ganglion.

gn.mx-md.Gas. - maxillo-mandibular portion of the Gasserian
ganglion.

gn.opth.Gas. - ophthalmic portion of the Gasserian ganglion.

mand.arch - mandibular arch.

max.proc. - maxillary process.

n.mand. - mandibular nerve.

n.max. - maxillary nerve.

n.olf. - olfactory nerve.

n.opth. - ophthalmic nerve.

rm.conn. - communicating ramus.

Plate VI.

fore brain

f. n.olf.

e

2.

bl.ves.

1.

n.ophth.

rm.com.n.

gn.eil.

gn.ophth.Gas.

gn.Gas.

gn.mx-md.
Gas.

hind brain

optic cup

n.max.

n.mand.

d.

c.

max. proc.

b.

a.

mand. arch

hyoid arch

for profit

100

5

100

100

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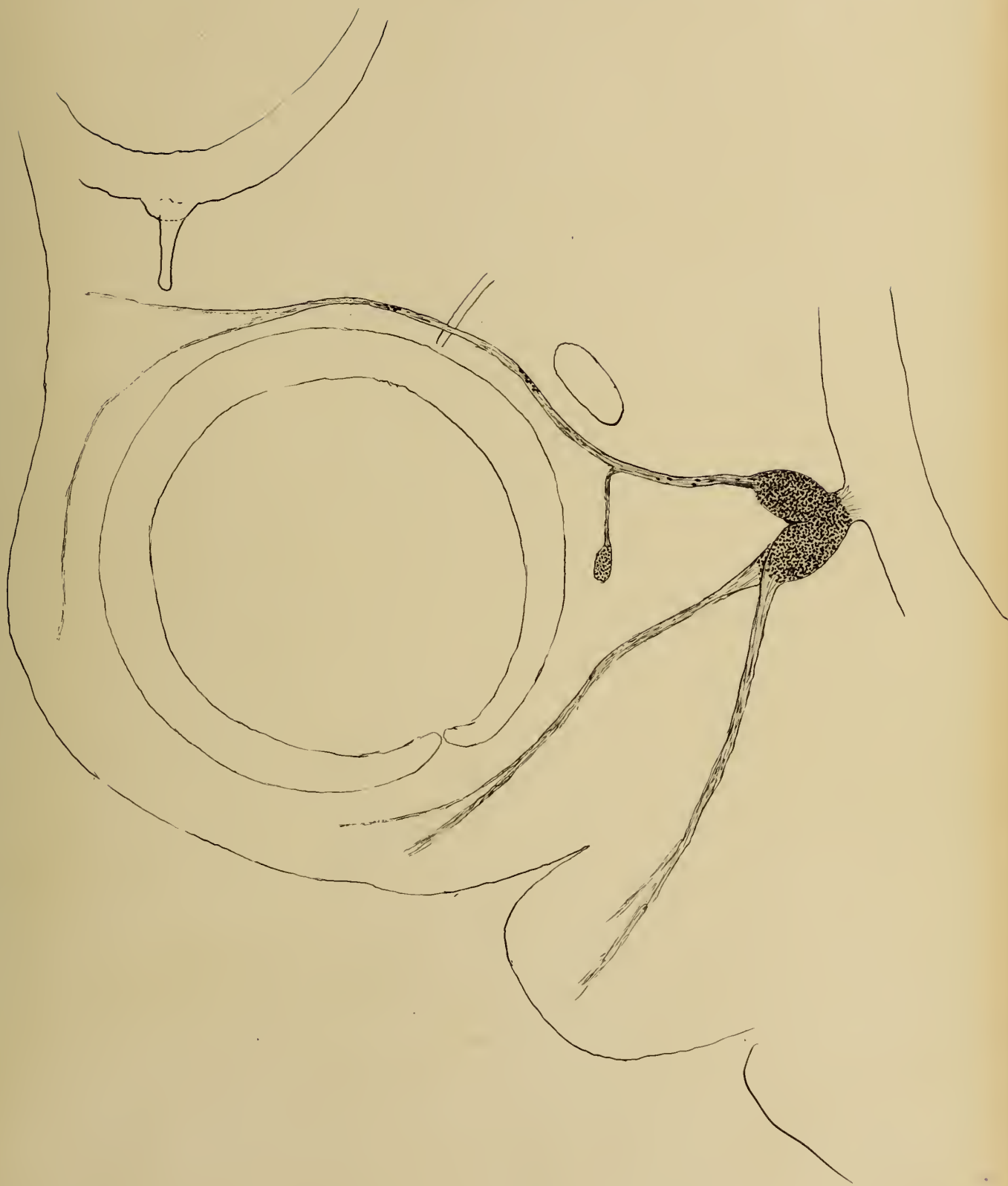
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Plate VI.

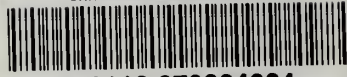


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